

Low connectivity between ‘scaly-foot gastropod’ (Mollusca: Peltospiridae) populations at hydrothermal vents on the Southwest Indian Ridge and the Central Indian Ridge

Chong Chen¹  · Jonathan T. Copley² · Katrin Linse³ · Alex D. Rogers¹

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Abstract Hydrothermal vents on mid-oceanic ridges are patchily distributed and host many taxa endemic to deep-sea chemosynthetic environments, whose dispersal may be constrained by geographical barriers. The aim of this study was to investigate the connectivity of three populations of the ‘scaly-foot gastropod’ (*Chrysomallon squamiferum* Chen et al., 2015), a species endemic to hydrothermal vents in the Indian Ocean, amongst two vent fields on the Central Indian Ridge (CIR) and Longqi field, the first sampled vent field on the Southwest Indian Ridge (SWIR). Connectivity and population structure across the two mid-oceanic ridges were investigated using a 489-bp fragment of the cytochrome oxidase *c* subunit I (COI) gene. Phylogeographical approaches used include measures of genetic differentiation (F_{ST}), reconstruction of parsimony haplotype network, mismatch analyses and neutrality tests. Relative migrants per generation were estimated between the fields. Significant differentiation ($F_{ST}=0.28–0.29$, $P<0.001$) was revealed between the vent field in SWIR and the two in CIR. Signatures were detected indicating recent bottleneck events followed by demographic expansion in all populations. Estimates of relative number of migrants were relatively low between the SWIR and CIR, compared with values between the CIR vent fields. The present study is the first to investigate connectivity between hydrothermal

vents across two mid-ocean ridges in the Indian Ocean. The phylogeography revealed for *C. squamiferum* indicates low connectivity between SWIR and CIR vent populations, with implications for the future management of environmental impacts for seafloor mining at hydrothermal vents in the region, as proposed for Longqi.

Keywords Deep-sea · Dispersal · Hydrothermal vent · Indian Ocean · Population connectivity · Scaly-foot gastropod

Introduction

Hydrothermal vents were first discovered in 1977 (Lonsdale 1977) along the Galapagos Rift (GAR) and typically host rich benthic communities containing a large proportion of vent-endemic species. As a result of continued discovery and sampling, it has become clear that hydrothermal vents in different regions of the world are characterised by different species compositions and different dominant taxa, forming distinct biogeographic provinces (Tunnicliffe 1991; Tunnicliffe et al. 1998; Ramirez-Llodra et al. 2007). Recent statistical modelling using multivariate regression trees recognised 11 hydrothermal vent provinces worldwide (Bachraty et al. 2009; Rogers et al. 2012). Elucidating how vent-endemic species disperse and maintain connectivity between different hydrothermal vent fields is important in understanding their biogeography and speciation. As well as their unique fauna, hydrothermal vent fields also hold rich mineral resources in the form of seafloor mass sulphides (SMS) containing high-grade polymetallic ores (Hannington et al. 2011), and recently, there has been a growing interest in their exploitation through deep-sea mining (e.g., Nautilus Minerals in Papua New Guinea and Bluewater Metals in Solomon Islands; Van Dover 2011a).

✉ Chong Chen
chong.chen@zoo.ox.ac.uk

¹ Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK

² National Oceanography Centre, University of Southampton, European Way, Southampton SO14 3ZH, UK

³ British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Distances between active vents on mid-ocean ridges and stability of these vents largely depend on the spreading rate (Hannington et al. 2011). Fast-spreading ridges such as the East Pacific Rise (EPR) have short distances of tens of kilometres between vents and a longevity of decades or less, whilst slow-spreading ridges like the Mid-Atlantic Ridge (MAR) have vents separated by hundreds to thousands of kilometres with a longevity of centuries or more (Vrijenhoek 2010). Connectivity between different vents and fields is maintained largely by larval dispersal (Van Dover 1990), which is influenced by a number of factors such as dispersal capability, life-history traits, oceanic currents, ocean temperature, vent geology, vent fluid chemistry and the presence of physical barriers (Vrijenhoek 2010). Much of the current knowledge on genetic connectivity between hydrothermal vents (reviewed in Vrijenhoek 2010) is based on the well-studied systems in the Pacific and Atlantic oceans such as EPR and MAR.

The Indian Ocean is the least studied of the three major oceans in terms of hydrothermal vents and other deep-sea ecosystems. The first vent field was not discovered until 2000 (Hashimoto et al. 2001; Van Dover et al. 2001): the Kairei field (25° 19.23' S, 70° 02.42' E), located on the Central Indian Ridge (CIR), which has an intermediate spreading rate of 50–60 mm year⁻¹, near the Rodriguez Triple Junction. Since then, three further vent fields have been discovered on the CIR: the Edmond (23° 52.68' S, 69° 35.80' E; Van Dover et al. 2001); Dodo (18° 20.10' S, 65° 17.90' E); and Solitaire (19° 33.41' S, 65° 50.89' E) fields (Nakamura et al. 2012). Kairei, Edmond and Solitaire are larger fields (area of hydrothermal emissions approx. 50 m by 50 m, Nakamura et al. 2012) with higher species richness, whilst Dodo is smaller (emission area approx. 10 m by 10 m, Nakamura et al. 2012) and only hosts a subset of the fauna found at the larger fields. The alvinocaridid shrimp *Rimicaris kairei* Watabe and Hashimoto, 2002 is one of the dominant species at these CIR vents, forming dense aggregations over black smoker chimney structures in Kairei, Edmond and Solitaire, and present in smaller patches on chimneys at Dodo. Other dominant faunas in Kairei include hairy snails (*Alviniconcha marisindica* Okutani, 2014), 'scaly-foot gastropods' (*Chrysomallon squamiferum* Chen et al. 2015a, b), mussels (*Bathymodiolus septemdierum* Hashimoto and Okutani, 1994, *B. marisindicus* Hashimoto, 2001 is a synonym; Vrijenhoek 2010; Fujikura et al. 2012), *Lepetodrilus* limpets, brachyuran crabs (*Austinograea rodriguezensis* Tsuchida and Hashimoto, 2002), stalked barnacles (*Neolepas* sp.) and large anemones (*Marianactis* sp.). The faunal assemblage at the Edmond vent field is similar but lacks the two large snails and stalked barnacles (Van Dover et al. 2001), whilst Solitaire is similar to Kairei in composition of dominant fauna alvinellid polychaetes are also present (Nakamura et al. 2012). At Dodo, the visually dominant species are *R. kairei*

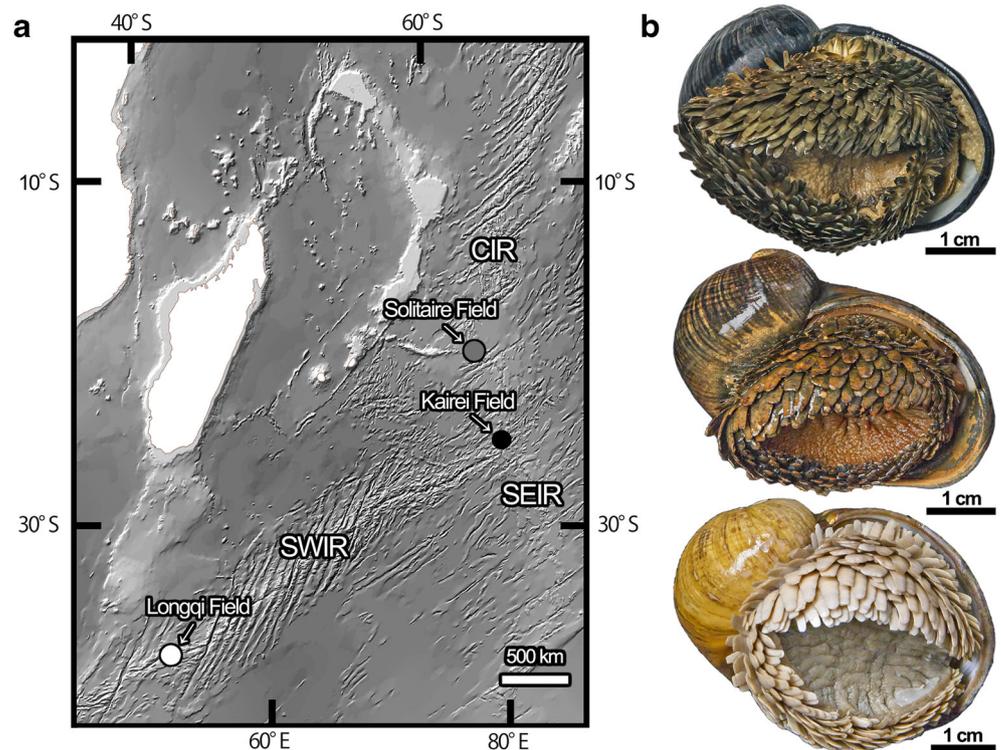
and *A. rodriguezensis* although *Marianactis* sp. anemones and *Lepetodrilus* limpets are also present (Nakamura et al. 2012). Watanabe and Beedessee (2015) give a checklist of known species in the four CIR fields.

In 2007, the first vent field was visually confirmed on the ultra-slow spreading (14–16 mm year⁻¹; Tao et al. 2014) Southwest Indian Ridge (SWIR) by expedition DY115-20 of the D/V *Dayang Yihao* was subsequently named the Longqi (also known as 'Dragon'; Roterman et al. 2013) vent field (37° 47' S 49° 39' E, Tao et al. 2012, 2014; Fig. 1a). The Longqi field is more than 2300 km away from Kairei, the closest neighbouring surveyed vent field, and more than 2500 km away from Solitaire (Tao et al. 2012), both lying beyond the intersection of the SWIR and CIR at the Rodriguez Triple Junction. The distance between Kairei and Solitaire is approximately 750 km along the CIR.

The recently discovered SWIR vent field provides the first opportunity to study across-ridge connectivity in the Indian Ocean. Tao et al. (2012) reported the presence of the 'scaly-foot gastropod' *C. squamiferum* (Mollusca: Peltospiridae) at the Longqi field based on visual observation. In November 2011, the first faunal samples were collected from the vent field during expedition JC67 of the RRS *James Cook*, using the remotely operated vehicle (ROV) *Kiel 6000* (Copley 2011). *C. squamiferum* is unique amongst gastropods in possessing numerous dermal sclerites which may be mineralised with iron sulphide, making it the only known living metazoan to incorporate iron in its skeleton (Warén et al. 2003; Chen et al. 2015a, b; Fig. 1b). These sclerites have been considered to either offer protection against predators/vent fluid or represent a by-product of sulphide detoxification, but their true function remains uncertain (Warén et al. 2003; Suzuki et al. 2006; Chen et al. 2015b). Also, unusual amongst chemosymbiotic molluscs is that it is a holobiont which houses a single strain of sulphur-oxidising symbiotic bacteria not in the gills but in a hypertrophied oesophageal gland, and *C. squamiferum* is considered to rely on these endosymbionts for nutrition (Goffredi et al. 2004; Nakagawa et al. 2014). First discovered at the Kairei field as a dark morphotype with dark shell and sclerites (Van Dover et al. 2001; Fig. 1b, middle), a light morphotype of this species is also known, with a yellowish shell and white sclerites from Solitaire in CIR (Nakamura et al. 2012; Fig. 1b bottom), and now also a third morphotype with brown shell and dark sclerites from Longqi (Chen et al. 2015a; Fig. 1b, top). Each morphotype is consistent and specific to the corresponding locality.

Connectivity of four dominant vent-endemic species at the CIR vents, including *C. squamiferum*, was investigated by Beedessee et al. (2013), revealing no genetic differentiation across all four known CIR sites, consistent with either panmixia or a recent range expansion. The presence of *C. squamiferum* on the SWIR now provides the opportunity to study the population structure of vent organisms in the Indian Ocean over a

Fig. 1 **a** Map of western Indian Ocean vent fields with *Chrysomallon squamiferum* records (Mollweide projection) created using ArcMap 10.1 (Esri 2012) with bathymetry data from GEBCO (BODC 2010). Abbreviations: SWIR South West Indian Ridge, CIR Central Indian Ridge, SEIR South East Indian Ridge. **b** Morphotypes of adult *C. squamiferum* specimens from Longqi (top), Kairei (middle) and Solitaire (bottom)



greater scale. This is important in terms of management of hydrothermal vent ecosystems as it provides a measure of the unique genetic identity and variation of individual populations, as well as their connectivity which may relate to the likelihood of recolonisation following disturbance (Van Dover 2011b; Van Dover 2014). The China Ocean Mineral Resources Research and Development Association (COMRA) signed a contract in 2011 with the International Seabed Authority (ISA) to explore SMS deposits on the SWIR for 15 years (Tao et al. 2014), with the Longqi field within the contracted area whilst the population connectivity of its fauna to other known Indian Ocean vent fields has yet to be determined. This study therefore aims to investigate the connectivity of three populations of *C. squamiferum* between two vent fields on the CIR and the first sampled vent field on the SWIR.

Materials and methods

Study materials

Specimens of *C. squamiferum* were collected from the Longqi hydrothermal vent field (Tao et al. 2014), SWIR (37°47.03'S 49°38.97'E), depth 2785 m, during the RRS *James Cook* cruise JC67 in November 2011 using the suction sampler of the ROV *Kiel 6000* (Copley 2011). Thirty-five specimens (sample code JC67-F-070/X) were randomly selected amongst specimens from a single suction event at 'Tiamat

Chimney', the only site where *C. squamiferum* was sampled during the expedition, were fixed and stored in 99 % ethanol for genetic investigations in the present study. In this particular site, *C. squamiferum* formed dense aggregations around diffuse flow venting.

Genetics

Partial sequences of the mitochondrial cytochrome oxidase *c* subunit I (COI) gene were used for the population genetic analyses in the present study. The sequences of *C. squamiferum* from the Longqi hydrothermal vent field, SWIR (Tao et al. 2014) were newly sequenced, whilst the sequences from the Kairei and Solitaire fields, CIR were obtained from the DNA Databank of Japan (DDBJ) under the accession numbers of AB540629 to AB540646, AB543244 to AB543246, AB634505 to AB634513 and AB691090 to AB691129. The total COI dataset comprised individual sequences of 35 specimens from the Longqi Field, SWIR, 35 specimens from the Kairei Field and 23 specimens from Solitaire Field, CIR (Table 1). The CIR data were also used in two previous studies (Nakamura et al. 2012; Beedessee et al. 2013). The newly obtained SWIR data are deposited in GenBank under accession numbers KT023265 to KT023299.

Genomic DNA was extracted using QIAGEN DNeasy Blood and Tissue Kit following the manufacturer's instructions (QIAGEN, Crawley, West Sussex, UK), and extractions were stored in -20 °C freezers. Quality checking of

Table 1 Statistical summary of *Chrysomallon squamiferum* COI gene data for the three localities

Population	Number	Haplotypes	Polymorphic sites	$h \pm SD$	$\pi \pm SD$
Longqi, SWIR	35	12	12	0.6689 \pm 0.0877	0.0031 \pm 0.0021
Kairei, CIR	35	18	18	0.8941 \pm 0.0438	0.0058 \pm 0.0035
Solitaire, CIR	23	12	22	0.8972 \pm 0.0404	0.0064 \pm 0.0038

h haplotype diversity, π nucleotide diversity, *SWIR* Southwest Indian Ridge, *CIR* Central Indian Ridge, *SD* standard deviation

extractions was carried out with the NanoDrop 2000 Spectrophotometer. Initially, the COI region of *C. squamiferum* was amplified with the primer pair LCO1490 and HCO2198 (Folmer et al. 1994) but several specimens required a species-specific primer pair for successful amplification: *SFIF* (5'-GATCTGGTCTTTTAGGAACA GGATTCA-3') and *SFIR* (5'-TGTGAGATACCATTCCTCAA ATCCAGG-3') (from Chen et al. 2015a). This latter set of primers amplified an approximately 500-bp fragment of COI.

Polymerase chain reaction was carried out in 12 μ L reactions, including 2 μ L DNA template (100–200 ng μ L⁻¹), 8 μ L QIAGEN Master Mix, 0.4 μ L double-distilled water, and 1.6 μ L primer mix containing 0.8 μ L each of forward and reverse primers at concentration of 4 pmol μ L⁻¹. Thermocycling was performed using the Bio-Rad C1000 Thermal Cycler, with the following protocol: Initial denaturation at 95 °C for 15 min was followed by 40 cycles of 94 °C for 45 s, 45 °C for 60 s, and 72 °C for 60 s and ended with final extension at 72 °C for 5 min. Amplification of desired region was confirmed using 1 % agarose gel electrophoresis stained with ethidium bromide (3 μ L of 10 mg mL⁻¹). PCR products were purified using QIAGEN QIAquick PCR Purification Kit (QIAGEN, Crawley, UK) using the manufacturer's protocol. Cycle sequencing reactions were carried out in 10 μ L volume, containing 0.5 μ L BigDye Terminator v3.1 (Applied Biosystems, Paisley, UK), 2.5 μ L 5 \times buffer, 2.5 μ L PCR product, 2.5 μ L primer (0.8 pmol μ L⁻¹), and 2 μ L double-distilled water. The following protocol was used: Initial denaturation at 96 °C for 1 min was followed by 25 cycles of 96 °C for 10 s, 50 °C for 5 s, and 60 °C for 4 min and ended with final extension at 60 °C for 4 min. Products were precipitated using the EDTA/ethanol method. Sequences were resolved from precipitated products using Applied Biosystems 3100 DNA sequencer (Paisley, UK) in the Department of Zoology, University of Oxford, UK.

Forward and reverse readings were assembled into contigs in the software package Geneious v5.6 (Drummond et al. 2011), and reads were manually quality-checked and corrected by eye. Only sequences with both good quality matching forward and reverse readings were used in downstream analyses. Population genetic inferences were made from the sequences using the software Arlequin v3.5.1.3 (Excoffier and Lischer 2010). Mismatch distribution analyses

and departures from equilibrium as expected for neutral markers were tested statistically using Tajima's D test (Tajima 1989) and Fu's F_S test (Fu 1997) in the same program, using 10,000 permutations. The statistical parsimony network was constructed using the software TCS v1.21 with the connection probability set to 95 % (Clement et al. 2000). The program Migrate-n v3.6.6 (Beerli 2009) was used to estimate relative migrants per generation with Bayesian inference. Length of COI fragments used for final population genetic inferences was 489 bp.

Results and discussion

Significant genetic differentiation was confirmed across the populations of *C. squamiferum*. In particular, pairwise F_{ST} estimates revealed significant genetic divergence between the Longqi, SWIR, field and the two CIR fields (Table 2). Both Longqi-Kairei pair ($F_{ST}=0.292$, $P<0.001$) and Longqi-Solitaire pair ($F_{ST}=0.280$, $P<0.001$) displayed significant genetic differentiation. The Kairei-Solitaire CIR pair ($F_{ST}=0.000$, $P=0.576$), in contrast, showed very little genetic divergence and appears to be well-mixed. This agrees well with results reported previously by Nakamura et al. (2012) and Beedessee et al. (2013).

A haplotype network (Fig. 2a) was reconstructed from the partial 489 bp COI sequences. Haplotypes from Longqi, SWIR, formed a discrete cluster from the CIR haplotypes, with one single shared haplotype between two individuals from Longqi and one individual from Solitaire. This haplotype

Table 2 Results of genetic structure analyses showing the fixation index (F_{ST}) with significance levels indicated

Population	Longqi, SWIR	Kairei, CIR	Solitaire, CIR
	Pairwise F_{ST}		
Longqi, SWIR	0.00000	–	–
Kairei, CIR	0.29180***	0.00000	–
Solitaire, CIR	0.28010***	0.00000	0.00000

SWIR Southwest Indian Ridge, *CIR* Central Indian Ridge

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

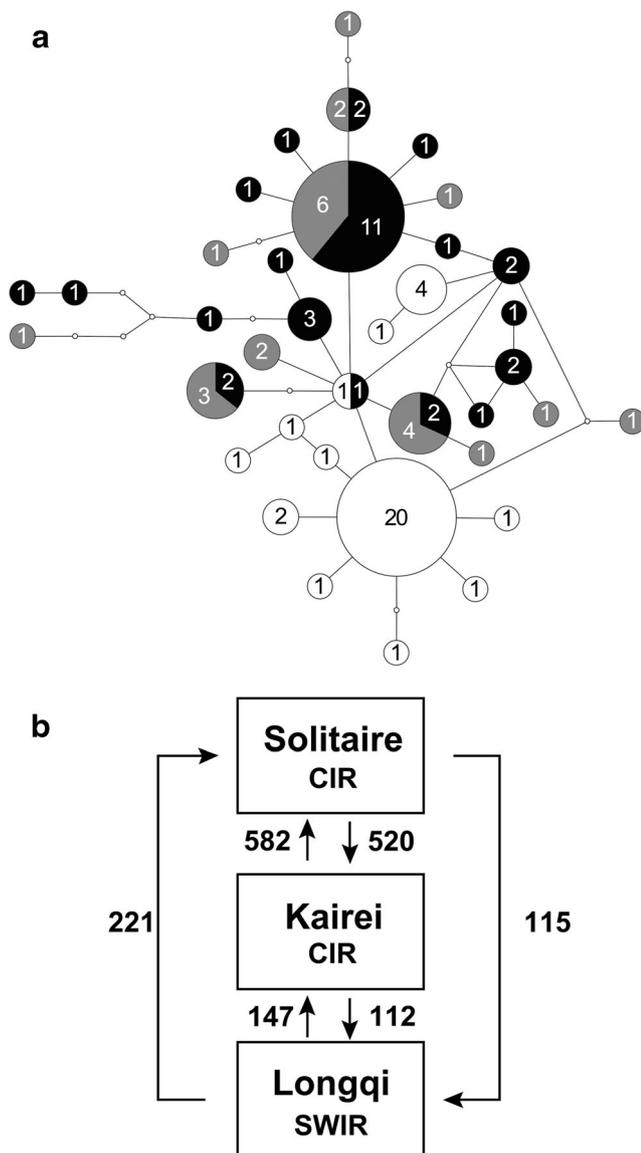


Fig. 2 **a** Parsimony haplotype network of *Chrysomallon squamiferum* based on 489 bp of the COI gene. Colours of circles indicate locality: white=Longqi, black=Kairei, and grey=Solitaire. Numbers indicate sampled frequency from each site. **b** Results of Migrate-n analyses showing relative migrants per generation shown in a schematic drawing. Abbreviations: SWIR Southwest Indian Ridge, CIR Central Indian Ridge

appears to link the two ridge systems in the network, and as the central haplotype represent older ones, CIR and SWIR populations may have been colonised from a common ancestral region where this haplotype was present. However, this may also be a result of homoplasy. There are two other haplotypes from SWIR nested within CIR that suggest further shared haplotypes are likely to exist but were not sampled. The dominant haplotype in the two CIR fields was the same but distinct from the SWIR population haplotypes. The results clearly show that the population of *C. squamiferum* from SWIR is genetically distinct from the population from CIR,

and we infer a low dispersal and connectivity across the vents on the two ridges. The two CIR populations share many haplotypes, as has already been previously reported (Beedessee et al. 2013).

Furthermore, results of Migrate-n analyses (Fig. 2b) estimated number of relative migrants per generation to be much lower between SWIR and CIR population (112–221) than between the two CIR sites (520–582). The predominant direction of dispersal in CIR is inferred to be from the southern Kairei to the northern Solitaire (582), which agrees with the previous study (Beedessee et al. 2013). Deep-ocean currents have strong influence on the predominant direction of dispersal in vent organisms as the larvae of many species are transported in them (Vrijenhoek 2010). A net northward flow in the deep currents of the area result from circumpolar deep water entering northwards into the Indian Ocean (Talley et al. 2011) may explain the trend of dispersal seen on the CIR, which is supported by data from investigating the hydrothermal plume spread over Kairei which showed a north to north-west direction (Noguchi et al. 2015). The gene flow direction between SWIR and CIR is inferred to be predominantly from SWIR to CIR (221 vs 115 from CIR to SWIR). The prevailing eastward Antarctic Circumpolar Current, Aghulas Current retroflexion and South Indian Current over SWIR (Talley et al. 2011) are likely to be the driving forces of this trend. These results are from single-gene only, however, and should not be considered conclusive. Future studies using further independent markers are warranted to confirm the preliminary results reported here.

The generally star-shaped haplotype network with many private haplotypes from both SWIR sites and the negative Fu's F_s (significant for Longqi and Kairei; Fu 1997) and Tajima's D (significant for Solitaire; Tajima 1989) statistics of neutrality tests (Table 3) are suggestive of departure from mutation-drift equilibrium (Table 3). Both haplotype and nucleotide diversities were lower in the SWIR population compared to the CIR population (Table 1). The mismatch analyses for all three fields revealed distributions without multiple peaks (Fig. 3). Divergence of mismatch distributions from the population expansion model was assessed sums of squared deviation (SSD) and raggedness index calculated based on sum of squares deviations between the model and observed distributions (Table 3). Both SSD and raggedness index indicated that the observed mismatch distributions in all populations were not statistically different at the 95 % confidence level ($P > 0.05$) from model predicted frequency. These results are consistent with a recent demographic expansion after a bottleneck, or a selective sweep. Such signatures seem to be the norm in the case of vent organisms. For the CIR populations, this is consistent with the previous reports by Beedessee et al. (2013). Previously reported results for the vent crab *A. rodriguezensis* and shrimp *R. kairei* of CIR also indicated similar demographic history (Beedessee et al. 2013), and

Table 3 Neutrality test statistics (Fu's F_S and Tajima's D) and mismatch distribution (SSD and raggedness index), with significance levels indicated

Population	Tajima's D	Fu's F_S	SSD	Raggedness
Longqi, SWIR	-1.4909	-6.5709***	0.0110	0.0494
Kairei, CIR	-1.1854	-10.5875***	0.0012	0.0153
Solitaire, CIR	-1.6579*	-3.0427	0.0131	0.0515

SWIR Southwest Indian Ridge, CIR Central Indian Ridge, SSD sum of squared deviations

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

similar results have been reported by hydrothermal vent-endemic animals of other oceans such as *Rimicaris exoculata* Williams and Rona, 1986 of Mid-Atlantic Ridge (Teixeira et al. 2011) and *Ifremeria nautilei* Bouchet and Warén, 1991 from the Manus Basin (Thaler et al. 2011). This reflects perhaps the demographic instability of vent metapopulations surviving across ephemeral patches (Vrijenhoek 2010).

Vent organisms have a great diversity of dispersal strategies (Vrijenhoek 2010) and may produce planktotrophic larvae that can rise up in the water column and feed to extend pre-settlement lifespan (e.g., *Bathymodiolus* mussels, *Rimicaris* shrimps) or lecithotrophic larvae which generally rely on yolk for nutrition (e.g., vesicomyid clams, neomphaline gastropods and vetigastropods, *Riftia* giant tube worms). Furthermore, some species brood their larvae (e.g., provannid gastropod *Ifremeria nautilei* Bouchet and Warén, 1991, amphipod *Ventiella sulfuris* Barnard and Ingram, 1990). In general, species with planktotrophic larvae have been shown to disperse further distances and maintain higher connectivity over long distances. *R. exoculata* populations have been shown to be well-connected over a ~7000 km stretch of the MAR (Teixeira et al. 2012), and a similar case has been reported in the *B. septemdiem* complex where the populations are well-connected across southwest Pacific to the CIR (Kyuno et al. 2009). In contrast, populations of *Riftia pachyptila* Jones, 1980 with lecithotrophic larvae show genetic differentiation

over the EPR which increased with geographical distance (Coykendall et al. 2011), and significant genetic differentiation was also shown for the EPR vent limpet *Lepetodrilus elevatus* McLean, 1988, also with lecithotrophic development (Plouviez et al. 2009). A number of potential dispersal barriers, such as transform faults, topographic depressions, fracture zones and current regimes, have been proposed (Vrijenhoek 2010), although the extent to which these restrict gene flow depends on a species' dispersal strategy.

The development of *C. squamiferum* is assumed to be lecithotrophic with a planktonic dispersal stage, which is the norm in Peltospiridae (Warén et al. 2006), although neither larvae nor intact protoconchs are yet known. Though lecithotrophic larvae do not preclude the possibility of long-distance dispersal (Marsh et al. 2001; Pradillon et al. 2001), the eggs of *C. squamiferum* are known to have a negative buoyancy under atmospheric pressure (Beedessee et al. 2013), suggesting a possible low dispersal ability compared with other species. Features such as fracture zones or depressions are likely to act as barriers of dispersal for this species (Creasey and Rogers 1999; Vrijenhoek 2010).

With only one site sampled, it is not currently possible to explore the dispersal and connectivity of *C. squamiferum* amongst other vent fields on the SWIR, but other active vent fields on the SWIR have been detected (e.g. 58.9° E, German et al. 1998; 63.9° E, Tao et al. 2009; 53.25° E and 51.01° E; Tao et al. 2014). It may be the case, however, that not all vent fields are suitable for *C. squamiferum* if their dependence on a nearly clonal gammaproteobacterial endosymbiont (Goffredi et al. 2004; Nakagawa et al. 2014) restricts them to vent fields in particular geological settings (Nakamura and Takai 2014). Future explorations of other SWIR vent fields will lead to better understanding of how this gastropod is distributed and to provide further insights into its genetic diversity, population connectivity and phylogeography on the SWIR.

The presented results strongly indicate that *C. squamiferum* population at Longqi, SWIR, may represent a genetically unique population amongst currently known Indian Ocean

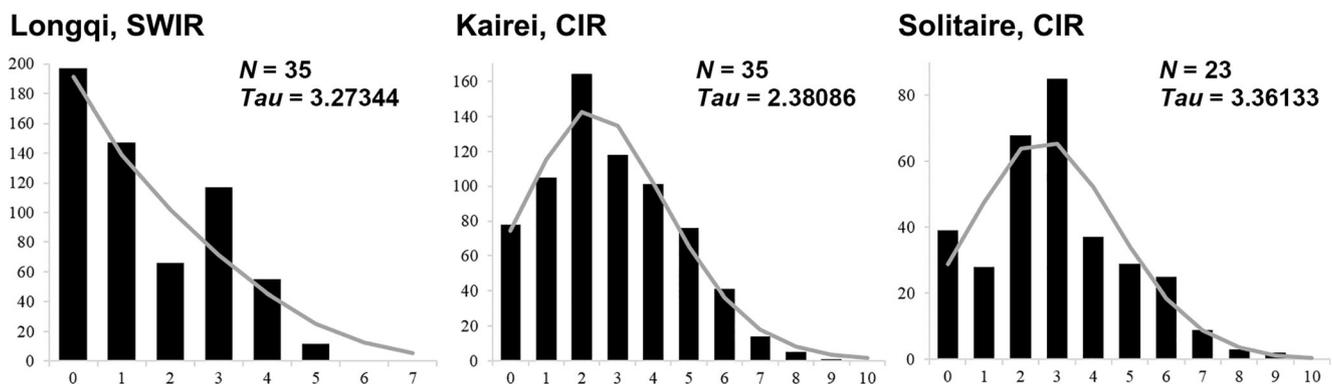


Fig. 3 Mismatch distribution of *Chrysomallon squamiferum* in the three localities with grey line showing model distribution; x-axis=pairwise difference and y-axis=frequency

vent fields. A limitation of the present study to be aware of is that all specimens from SWIR were taken from a single sampling event at Longqi, and thus, it is difficult to judge, based on current data, if the observed genetic diversity in Longqi is representative of the whole SWIR area. The presence of distinct haplotypes from CIR may be partly due to genetic drift within SWIR. These data are, nevertheless, the only data currently available until future expeditions to sample further SWIR vent fields. In addition to taxa shared with CIR vents such as *C. squamiferum* and *R. kairei*, a number of taxa new to science were discovered at the Longqi field, for example, an undescribed species of *Kiwa* yeti crab (Roterman et al. 2013) and an undescribed large-sized peltospirid gastropod (Chen et al. in press) with affinities to vent communities at the East Scotia Ridge in Antarctica (Rogers et al. 2012). With the potential for COMRA's exploitation of SMS in the SWIR vents planned for the very near future (Tao et al. 2014), these population genetic results may have implications for management of the Longqi site and possibly other sites on the SWIR (Van Dover et al. 2014). What is clear is that SWIR vent communities are different to the CIR and the exact consequences of mineral extraction will remain unclear until further observations and sampling are undertaken for other vent sites between 46° E and 53° E. Such exploration is a prerequisite to the design of appropriate long-term environmental monitoring and management measures for deep-sea mining in this region.

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Conflict of interest The authors declare that they have no competing interests.

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